ONTOGENETIC POLYCHROMATISM IN MARSUPIAL FROGS (ANURA: HYLIDAE)

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and
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ABSTRACT

Color polymorphism is common in many species of marsupial frogs. Extreme cases of pattern polymorphism are documented in four species. In *Amphignathodon guentheri, Gastrotheca aureomaculata, G. griswoldi,* and *G. helenae* juveniles are known to have only one color morph, where as two or more patterns exist in adults. In these species, polymorphism apparently develops ontogenetically.

RESUMEN

El polimorfismo cromático es común a algunas especies de sapos marsupiales. Casos extremos del modelo de polimorfismo son evidentes en cuatro especies *Amphignathodon guentheri, Gastrotheca aureomaculata, G. griswoldi,* y *G. helenae.* En estas especies, se sabe que los juveniles tienen sólo un morfo de color; el polimorfismo, al parecer, se desarrolla ontogenéticamente.

During our independent field work on marsupial frogs of the genera *Amphignathodon* and *Gastrotheca,* we have noted striking differences in color patterns among adults within single populations. Furthermore, maintenance of broonding females until the birth of the young has provided data on the color patterns of single broods of young; similar comparisons have been made between juveniles and adults obtained in the field.

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Here in we provide observations on color polymorphism in four species of marsupial frogs and discuss the possible mechanisms responsible for this polychromatism.

Amphignathodon guentheri Boulenger.

This large arboreal species (♂♂ to 75 mm; ♀♀ to 82 mm snout-vent length) inhabits Andean cloud forests in Ecuador and southwestern Colombia. Twenty adults and subaldults have been examined. Ten (3 ♂♂, 7 ♀♀) of these have a tan dorsum with longitudinal dark streaks; eight (6 ♂♂, 2 ♀♀) are dark brown to grayish black with pale spots (red in life in at least two individuals), and two (1 ♂, 1 ♀) are uniform green (Fig. 1). All three color morphs have been collected in one ravine (Quebrada Zapadores, 5.5 km ESE Chiriboga, 2010 m, Provincia Pichincha, Ecuador). Eleven newly born juveniles are known. All were uniform green in life. They were collected at the Reserva Natural La Planada, 7 km S Chucunés, Departamento Nariño, Colombia; three adults from the same locality were tan with longitudinal dark marks.

Gastrotheca aureomaculata Cochran and Goin.

This moderately large species (♂♂ to 72 mm; ♀♀ to 76 mm snout-vent length) lives in cloud forests on the eastern slopes of the Cordillera Central in southern Colombia. Duellman (1983) noted two color patterns among 28 adults from the vicinity of Moscapán, 2050 m, Departamento Huila, Colombia. Thirteen adults (9 ♂♂, 4 ♀♀) were dark brown to black with pale spots; 15 (7 ♂♂, 8 ♀♀) were olive-tan to green with no pale spots (Fig. 2). Cochran and Goin (1970) mentioned that one brooding spotted female obtained at Moscapán produced tadpoles in the laboratory that metamorphosed in to uniformly green frogs.

Gastrotheca griswoldi Shreve.

This small terrestrial species (♂♂ to 40 mm; ♀♀ to 44 mm snout-vent length) inhabits dry puna grasslands at elevations of 3000 to 4020 m in the region of the Nudo de Pasco in the Andes of central Perú. Examination of 235 adults and subadults revealed that all had a tan or gray dorsum with dark brown, gray, or olive-green markings. Thirty-eight juveniles were collected at 32 km S of La Oroya, Departamento Junín, Perú, on 20 February 1979. Sixteen of these were uniform green with snout-vent lengths of 14.8-19.5 ($\bar{X} = 17.0$, SD = 1.71) mm; 22 were uniform brown or gray with snout-vent lengths of 17.5-20.7 ($\bar{X} = 19.0$, SD = 1.05) mm. The green juveniles are significantly smaller than the gray and brown ones (ANOVA, $P < 0.005$). Thus, it seems that in this species, recently hatched young are uniform green and by the time they have grown to an average length of 19 mm their color changes to gray or brown; later, the dark pattern develops.

Gastrotheca helenae Dunn.

This moderate-sized species (♂♂ and ♀♀ to 65 mm snout-vent length) is known only from 12 adults, all from Cerro Tamá on the Colombian-Venezuelan border. Ten individuals (7 ♂♂, 3 ♀♀) are tan with dark brown longitudinal markings on the dorsum; two individuals (1 ♂, 1 ♀) are dark brownish black with orange or yellow flecks on the dorsum (Fig. 4). The female that was dark brown with yellow flecks (ICN 10548) gave birth to 12 young, all of which were creamy tan with brown markings dorsally (Fig. 5).

DISCUSSION

The data presented here on color polymorphism involve two distinct phenomena (1) pattern polymorphism among adults within populations, and (2) pattern polymorphism between juveniles and adults. The former is common among species of the leptodactylid frog genus *Eleutherodactylus* (LYNCH, 1966; SAVAGE and EMERSON, 1970), and the inheritance of color patterns has been determined for some of the West Indian species of that genus (GOIN, 1950, 1954). Results of numerous breeding experiments have provided an understanding of the mechanisms of inheritance of color patterns in *Rana,* especially the color morphs of *R. pipiens* (see RICHARDS and NACE, 1983, for review).

Colors are determined by chromatophores. BAGNARA *et al* (1979) summarized evidence that the different kinds of pigment cells are derived from a stem cell containing a primary organelle. Cues present in the developing tissue dictate whether a given stem cell will become a melanophore, iridophore, or xanthophore. Differentiation of a stem cell in to a specific chromatophore can be controlled genetically, hormonally, or environmentally (RICHARDS and NACE, 1983).

The mechanisms of color pattern inheritance are not known in these marsupial frogs, but several possibilities exist.

RICHARDS (1982) demonstrated that sex hormones altered chromatophore expression in *Hyperolius viridiflavus* and that color pattern change in that species was associated with gonadal development and the presence of sex hormones. Possibly the ontogenetic change in coloration from juveniles to adults in all *G. griswoldi* is under hormonal control. No gonads could be distinguished in the small green juveniles, but gonads are differentiated in the brown and gray individuals having snout-vent lengths greater than 19 mm. On the other hand, some adults of *A. guentheri* and *G. aureomaculata* retain the juvenile coloration, whereas other adults of these species develop entirely

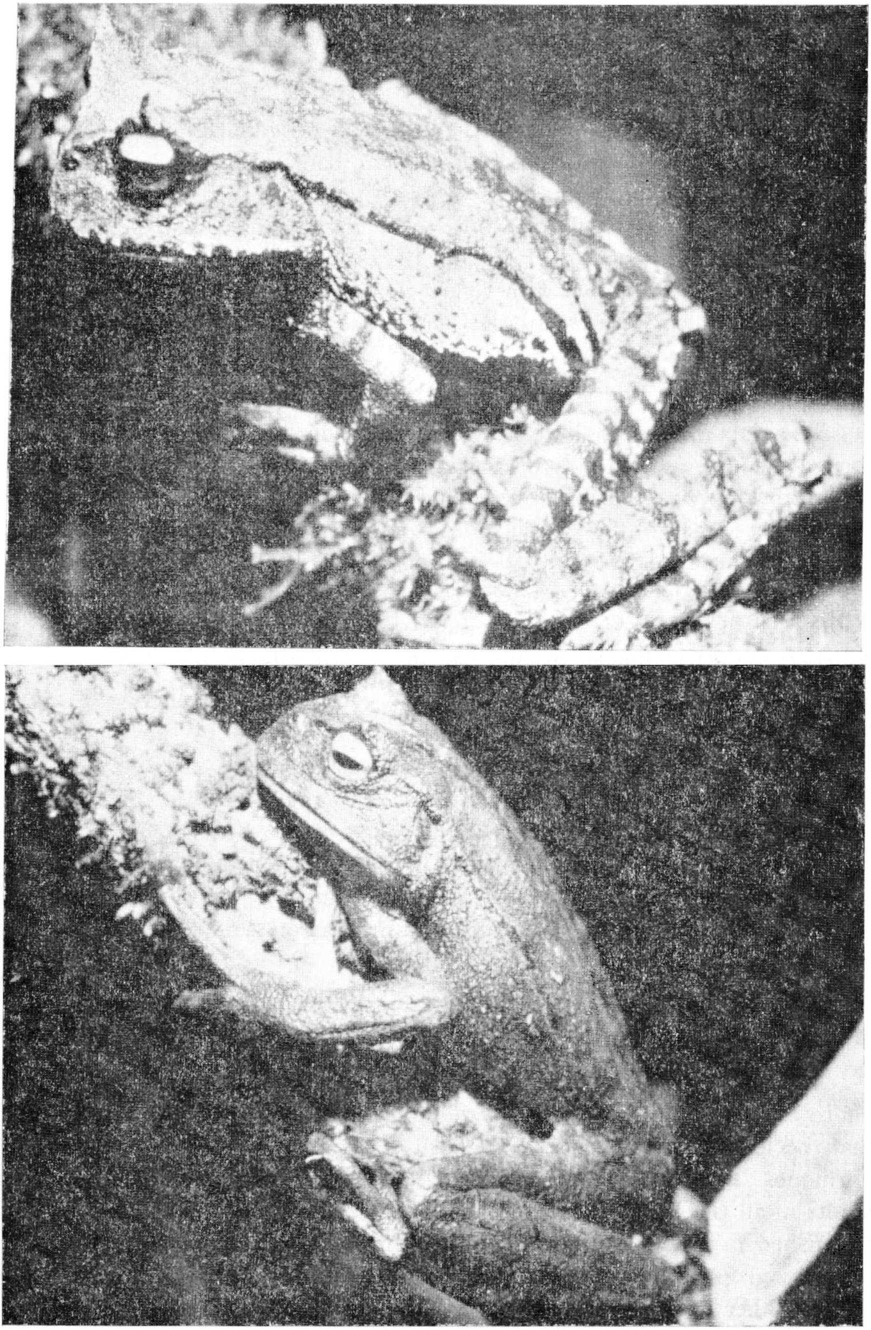


FIGURE 1 a-b.

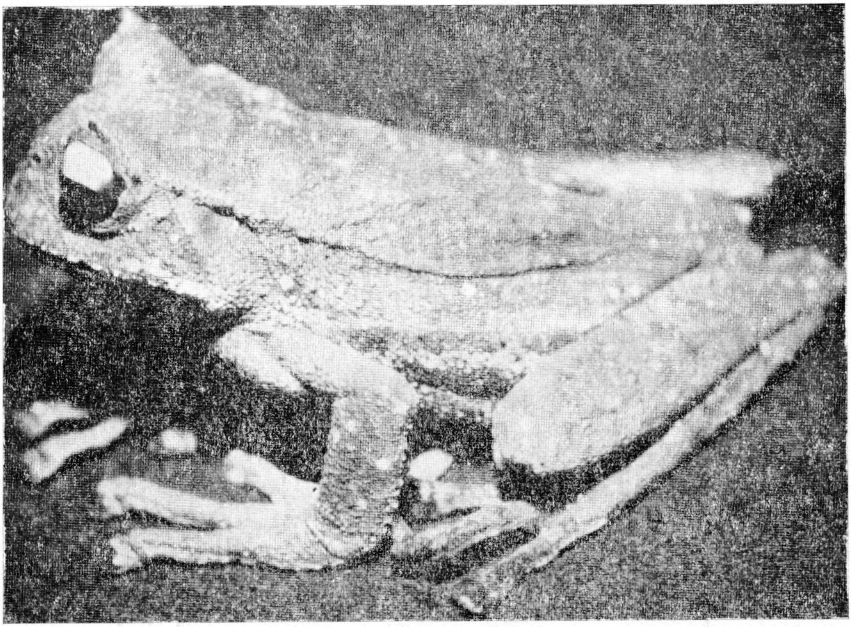


FIGURE 1 c.

Color morphs of *Amphignathodon guentheri* from Quebrada Zapadores, Ecuador: Top. Tan and brown-streaked morph, KU 164226, ♀, 74.7 mm snout-vent length. Middle. Black and red-spotted morph, KU 164224, ♂, 67.8 mm snout-vent length. Bottom. Green morph, KU 164228, ♀ 82.00 mm snout-vent length.

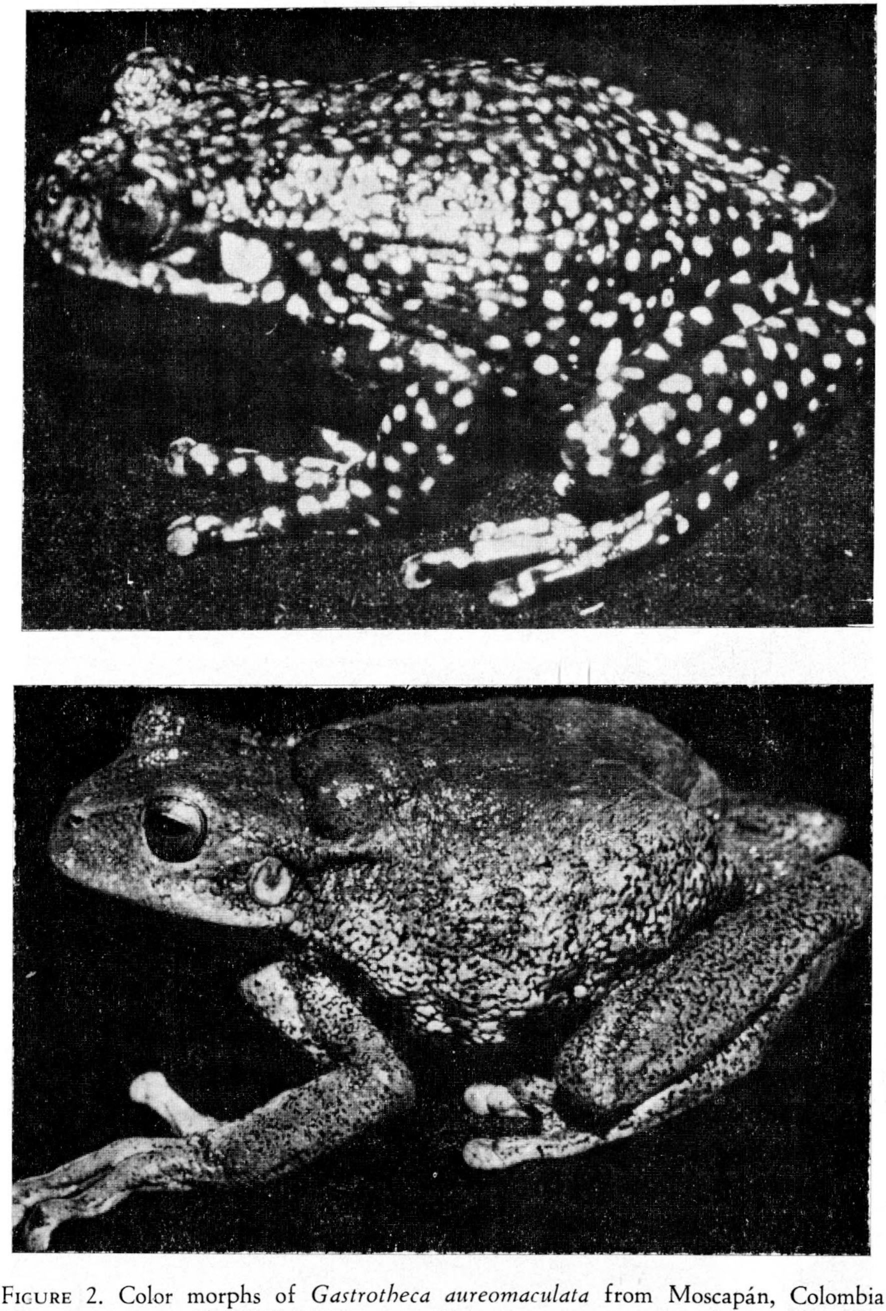
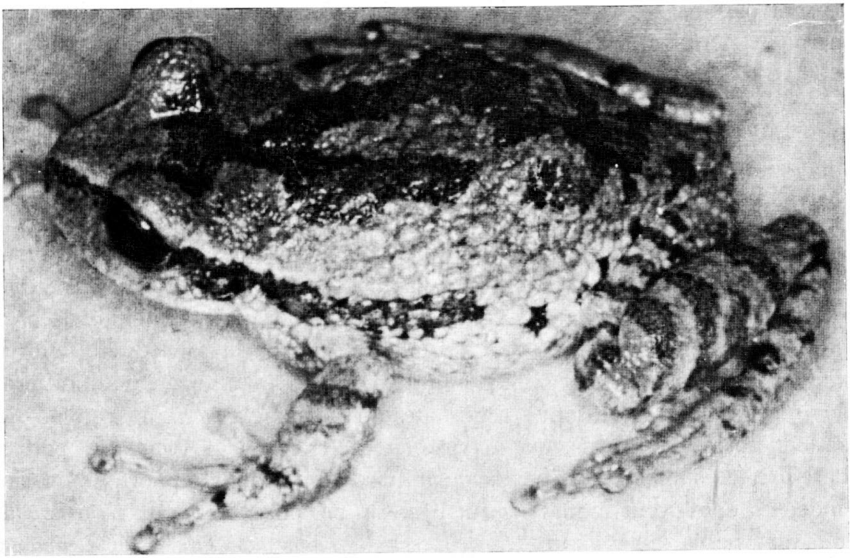


FIGURE 2. Color morphs of *Gastrotheca aureomaculata* from Moscapán, Colombia: Top. Spotted morph, KU 181194, ♂, 64.4 mm snout-vent length. Bottom. Plain green morph, KU 181196, ♀, 75.4 mm snout-vent length.



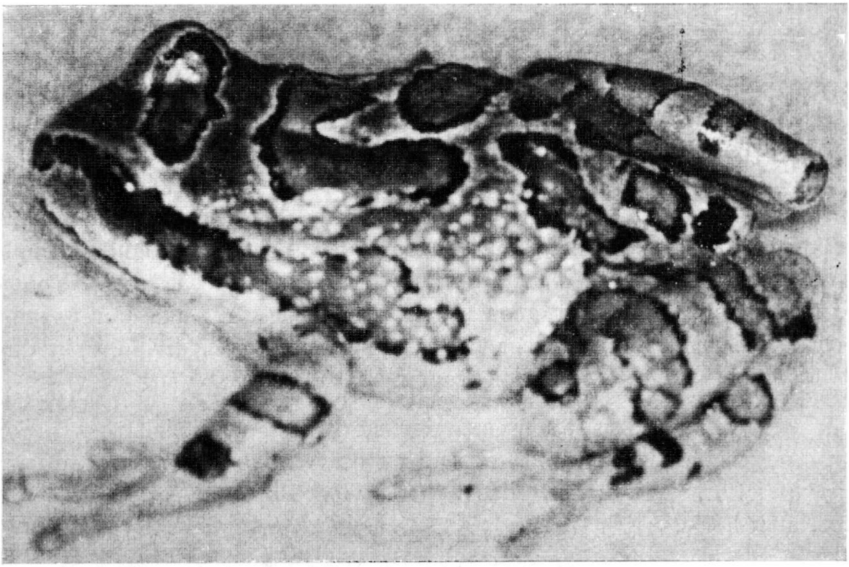


FIGURE 3. Color morphs of *Gastrotheca griswoldi* from the vicinity of La Oroya, Peru: Top. KU 139140, ♀, 38.7 mm snout-vent length. Bottom. KU 139152, ♂, 32.8 mm snout-vent length.

different patterns. If ontogenetic change in color pattern is under hormonal control in *A. guentheri* and *G. aureomaculata,* the hormones apparently do not have the same effect on all individuals. Given the numbers of individuals of each sex having different color patterns, it is evident that adult color pattern is not sex-linked in marsupial frogs. Furthermore, all adults examined seem to have normal gonads, as revealed by gross structure; therefore, there is no evidence that any individuals were hormonally deficient.

Some individuals of all of the species studied were collected during the breeding season, and others were taken at other times of the year; there is no evidence for seasonal change in color pattern. Living individuals of all of the species were observed over periods of several days to 18 mo with no changes in color patterns among adults. Because individuals with different color morphs have been found repeatedly in the same habitat at a given site, there is no reason to suspect environmental control of the color pattern. Therefore, we suggest that hormonal influence on chromatophore expression, if indeed it does occur in marsupial frogs, can be consistent, as in *G. griswoldi.* Or it may be variable, as in *A. guentheri, G. aureomaculata,* and *G. helenae,* in which cases possibly there is a null allele at the hormonally influenced locus that results in the retention of the juvenile coloration. On the other hand, color pattern inheritance in *G. helenae* might be a simple Mendelian system-involving a single locus with the felcked pattern bein a homozygous recessive.

Although some other species of *Gastrotheca* exhibit intrapopulational pattern polymorphism, none of these is known to undergo an ontogenetic change in pattern. For example, *G. excubitor* in the Andes of Perú has many color variants; these variants occur in approximately the same proportions in juveniles and adults (DUELLMAN and FRITTS, 1971). The color and pattern of *G. riobambae* are highly variable (DUELLMAN, 1973), but the proportions of laboratory-reared young aproximate those of the adults sampled at the same locality. On the other hand, some other species of *Gastrotheca* are remarkably uniform in color and pattern throughout life. For example, there is little variation in color pattern in *G. ovifera;* individuals in three lots of young were colored like their mothers.

These limited observations on color morphs of marsupial frogs suggest that ontogenetic changes might depend on differential responses of different genotypes to sex hormones. This hypothesis needs to be tested by genetic experiments.

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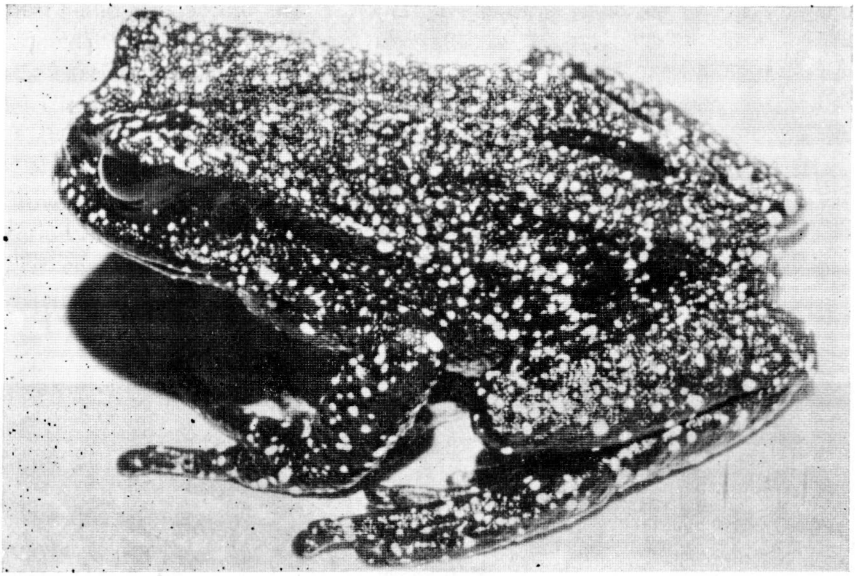

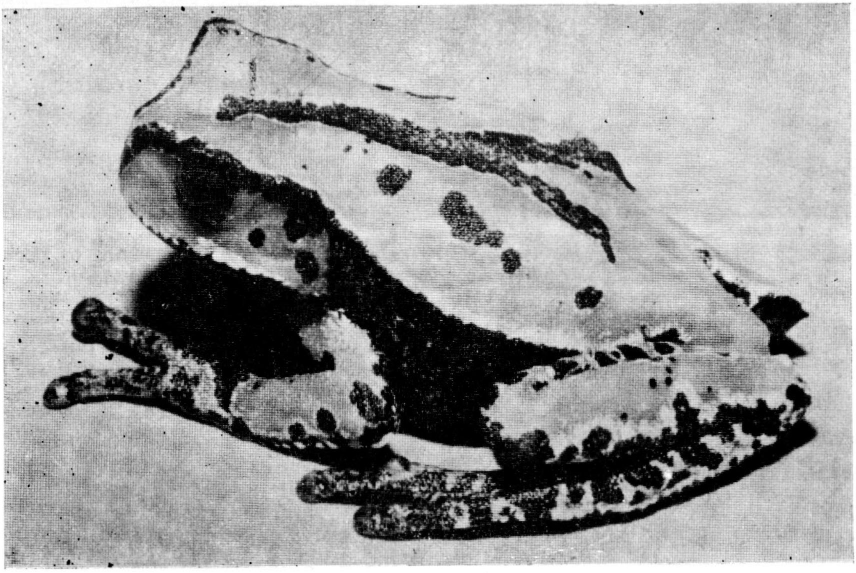

FIGURE 4. Color morphs of *Gastrotheca helenae* from Cerro Tamá, Colombia: Top. Flecked morph, ICN 10548, ♀, 64.9 mm snout-vent length. Bottom. Striped morph, ICN 10545, ♂, 65.0 mm snout-vent length.

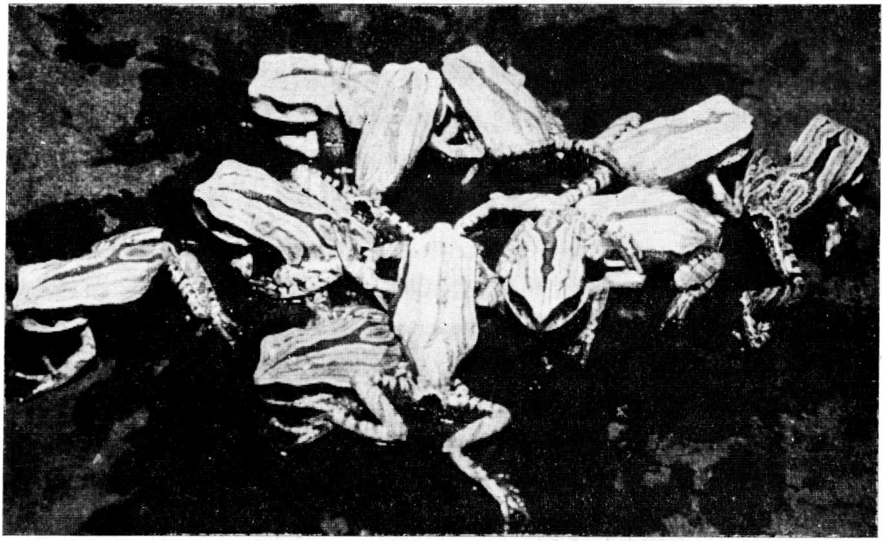

FIGURE 5. Eleven of 12 young *Gastrotheca helenae* (ICN 10552-62) born to flecked female, ICN 10548. See figure 4.

gator) and was accomplished in part in facilities provided by the Center for Biomedical Research at The University of Kansas. Work on *G. helenae* was carried out under grants to PEDRO M. RUÍZ-C. from the Facultad de Ciencias de la Universidad Nacional de Colombia and from COLCIENCIAS. Specimens cited by acronym are in the following collections: ICN = Instituto de Ciencias Naturales, KU = Museum of Natural History, University of Kansas. We are grateful to PATRICIA A. BURROWES for information on juvenile *Amphignathodon,* SALLY K. FROST and LINDA TRUEB for their constructive comments on the manuscript, and John E. Simmons for preparing the photographic prints.

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